STUDIES IN THE GRAMINEAE

IX. THE GRAMINEAE OF THE ALPINE REGION OF THE ROCKY MOUNTAINS IN COLORADO

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(WITH FIVE FIGURES AND PLATE XXX)

The object of the present paper is to offer a small contribution to the knowledge of the alpine vegetation of the Rocky Mountains, which I explored during the summers of 1896 and 1899. It is the intention especially to present some data in regard to the geographical distribution and to make a comparison between the grass vegetation of these mountains and that of mountains in the Old World; also that of the polar regions, which I had the opportunity to visit as a member of three Danish expeditions. Furthermore, I thought that a comparison of the alpine species with those from the wooded belts and the plains of Colorado might be of some interest; and finally a brief anatomical description of the alpine types has been inserted, since thus far the Gramineae have been much neglected in works dealing with structures of alpine plants. It will be seen that the geographical distribution of these species shows several points of interest, more so than their structure; nevertheless, to do full justice to the study of the anatomical characteristics of alpine plants, a consideration of all the families that are represented in these regions is necessary, even if the monocotyledons are of less importance on account of the frequent uniformity in their internal structure.

The exact number of alpine species in Colorado is of course not known; the wild country is very far from being well explored, and the literature is scanty. A very instructive paper was published by Parry,[1] however, who gives a long list of species from these regions, among which 56 species are said to be confined to the bald exposures above the timber line, while 86 others are also to be found at lower

[1] PARRY, C. C., The Rocky Mountain alpine region. Am. Ass. Adv. Sci. **18**: 248; see also PORTER and COULTER, Synopsis of the flora of Colorado. Washington. 1874; GRAY and HOOKER, The vegetation of the Rocky Mountain region. Bull. U. S. Geol. Survey **6**: No. 1. 1880.

elevations. According to this author 58 of these species occur also in the European and Asiatic mountains, or in high northern latitudes of both hemispheres. He enumerates 9 Gramineae. Among the 168 species of flowering plants I collected in this region only 17 belong to the Gramineae. The largest family is the Compositae with 25 species; then follow the Cyperaceae with 20, and then the Gramineae. Just above timberline the vegetation is luxuriant to the full extent of the word, and a number of very different plants abound in the willow-thickets along the mountain brooks; at higher elevations we may observe a rich vegetation on the slopes, especially near the snowbanks; but when we cross the bowlder fields we meet only with a very scant, often extremely poor, vegetation. Among the plants which were observed on the very summit of these mountains may be mentioned *Poa Lettermanni, Festuca ovina supina, Claytonia megarrhiza, Stellaria umbellata,* etc., but none of the Cyperaceae. It seems as if the Gramineae are able to thrive at very high elevations, judging from the various records of alpine plants in Europe and Asia, as will be shown later. It might be stated at the same time that some of these are among those that occur in the most northerly points; for instance, *Alopecurus alpinus* at 83° 4′, *Poa flexuosa* at 82° 50′, and *Festuca brevifolia* at 82° 27′.

In the accompanying Table (I) I have enumerated the alpine species of Gramineae, which I collected on the following mountains: Long's Peak, James' Peak, Pike's Peak, Mt. Elbert, Mt. Massive, Mt. Kelso, Gray's Peak, and along the headwaters of Clear Creek. To these may be added *Deschampsia calycina* Presl. from the summit of Gray's Peak, collected by B. H. Smith; and *Poa Pattersoni* Vas. from mountains near Gray's Peak, collected by H. N. Patterson. The altitude where these alpine species occur lies between 3350 and 4300^{m}. *Agrostis canina* var., *A. varians, Avena Mortoniana, Poa flexuosa, P. gracillima, P. Fendleriana, P. Lettermanni, P. Pattersoni, P. alpina, Festuca ovina supina, Deschampsia calycina, Agropyrum Scribneri,* and *A. violaceum* are in Colorado confined to the alpine region. The remaining species, on the other hand, were also observed at lower elevations, from the aspen zone (about 2500^{m}) to the spruce zone (about 3100^{m}). *Phleum alpinum,* for instance, descends to the aspen zone on Long's Peak, where it is very frequent in swamps; *Calamagrostis purpurascens* follows the creeks throughout the spruce zone on Long's Peak and the region of Clear Creek Canyon; *C. canadensis acuminata* is only exceptionally alpine, and thrives best in the swamps of the aspen zone; *Deschampsia caespitosa* is most frequent and typically developed in the swamps of the aspen zone,

TABLE I

Alpine Gramineae from Colorado	Long's Peak	James' Peak	Pike's Peak	Mt. Elbert	Mt. Massive	Mt. Kelso	Gray's Peak	Headwaters of Clear Creek
Phleum alpinum L.*	..	..	..	+	+	..	..	..
Agrostis varians Trin	+	+	..	..	..	..	..	..
A. canina L. var	..	..	..	..	+	..	..	..
Calamagrostis purpurascens R. Br	+	..	..	..	+	..	+	..
C. canadensis acuminata Vas	..	..	..	..	..	+	..	..
Deschampsia caespitosa Beauv	..	+	..	..	+	+	+	+
Trisetum subspicatum Beauv	..	+	..	+	+	+	..	..
Avena Mortoniana Scribn	..	+	..	..	..	..	..	..
Poa rupicola (Vas.) Nash	..	..	..	+	+	..	+	..
P. flexuosa Wahl	+	..	..	+	..	+	+	..
P. gracillima Vas	..	..	..	..	..	+	..	..
P. Fendleriana (Steud.)	..	+	..	+	..	..	+	..
P. alpina L	+	..	..	+	+	+	..	..
P. Lettermanni Vas	..	..	+	..	..	..	..	..
Festuca ovina L	+	+	..	+	+	+	..	..
F. ovina supina Hack	+	..	+	+	..	..	+	..
Agropyrum violaceum Lge	..	..	..	..	..	+	..	..
A. Scribneri Vas	+	+	..	+	..	..	+	..

* A + indicates the presence of the species, dots its absence.

but it is also very common near the snowbanks at high elevations; *Trisetum subspicatum* does not descend much farther than just to the timberline; *Poa rupicola* descends to the aspen zone on James' Peak and near Central City, but only seldom; *Festuca ovina* was collected in the aspen zone near Central City, and in the spruce zone on Mt. Massive and Long's Peak.

The distribution of these alpine species on the Pacific and Atlantic coasts is shown in Table II.

It will be seen from this list that of the 20 alpine species from Colorado 13 occur also on the Pacific coast, and 7 on the Atlantic, where they are either alpine or arctic, with the exception of *Deschampsia calycina.* Only 9 of these occur also in the Old World. Table III shows their distribution in the polar regions, in the northern parts of Europe and Asia, but south of the arctic, and in the mountains farther south.

TABLE II

	Pacific	Atlantic
Phleum alpinum	+	+
Agrostis varians	+	..
Calamagrostis purpurascens	+	..
C. canadensis acuminata	+	+
Deschampsia caespitosa	+	+
D. calycina	+	..
Trisetum subspicatum	+	+
Poa flexuosa	+	+
P. gracillima	+	..
P. Fendleriana	+	..
P. alpina	+	+
P. Lettermanni	+	..
Festuca ovina supina	+	+

TABLE III

	Polar regions														
	Arctic America	Greenland	Spitzbergen	Finmark	Russia	Novaja Zemlja	Siberia	Iceland	Faeroe Islands	Great Britain	Alps and Pyrenees	Caucasus	Bajkal' and Altai Mts.	Himalaya	Asiatic coast of Bering Strait
Phleum alpinum	+	+	..	+	+	..	..	+	..	+	+	+	+	+	+
Calamagrostis purpurascens	+	+	..	..	..	..	..	..	..	..	..	..	..	..	..
Deschampsia caespitosa	..	..	..	..	+	..	+	+	+	+	+	+	+	+	..
Trisetum subspicatum	+	+	+	+	+	+	+	+	..	..	+	+	+	+	+
Poa flexuosa	+	+	+	+	+	+	+	..	..	..	..	..	+	+	+
P. alpina	+	+	+	+	+	+	+	+	+	+	+	+	+	+	..
Festuca ovina	+	+	+	+	+	+	+	+	+	+	+	+	+	..	+
F. ovina supina	+	+	+	+	+	+	+	..	..	..	..	..	..	..	+
Agropyrum violaceum	+	+	..	+	..	..	+	..	..	..	..	..	..	..	..

Four of these are circumpolar: *Trisetum subspicatum, Poa flexuosa, P. alpina,* and *Festuca ovina,* also the var. *supina. Calamagrostis purpurascens* is the only one that is confined to this continent and Greenland; *Agropyrum violaceum* occurs in the arctic regions of both hemispheres, and var. *supina* of *Festuca ovina* is also an inhabitant of these high northern regions outside America. All the others extend to the mountains farther south, and five of these have even reached the Himalayas. According to CHEESEMAN,[2] *Deschampsia caespitosa macrantha* Hack. and *Trisetum subspicatum* occur in New Zealand, and the latter has also been recorded from the antarctic regions. *Deschampsia caespitosa* is in Arctic America, Greenland, Novaja Zemlja, and Arctic Siberia, mostly represented by vars. *brevifolia* Trautv. and *borealis* Trautv. *Agrostis canina* occurs in Greenland and in several forms, but the variety which I collected in Colorado is not among these. Professor HACKEL, who has kindly examined my specimens of Agrostis, thinks that my alpine *A. canina* is nearest to var. *pusilla* Aschers. et Graebn.

Tables II and III thus demonstrate the fact that the alpine Gramineae in Colorado represent an assemblage of several very distinct geographical types: some that are endemic to this particular region; some that occur also on the Pacific and Atlantic coasts; some that have reached the polar regions in certain parts of both hemispheres; some that are circumpolar; and finally some that have become dispersed throughout the mountainous districts farther south in Europe and Asia. Of the 20 species enumerated from the mountains of Colorado, 7 are arctic-alpine types. *Deschampsia caespitosa* and *Festuca ovina* are quite frequent in these alpine and arctic regions, but their widest distribution is within the lowlands of the temperate zones of both hemispheres; hence they are not "arctic-alpine" in the strict sense of the word.

The tribes that are thus represented in this alpine region are AGROSTIDEAE (5 spp.), AVENEAE (4 spp.), FESTUCEAE (8 spp.), and HORDEAE (2 spp.). They are represented by genera that are really cosmopolitan, and from Table III we have seen that some of the species are widely distributed in both hemispheres. These data alone might suffice to illustrate the principal points in regard to composition and geographical distribution; but in order to make the illustration more complete, it seems necessary to extend our comparison to the grass vegetation in the timbered belts and on the plains below; also to the vegetation of alpine regions of other mountains.

Beginning with the species of the spruce zone, it has been stated that some of the alpine species are found among them, where they become associated with a few types characteristic of the zone; and

[2] CHEESEMAN, T. F., Manual of the New Zealand flora. 1906.

with some others which are common also to the aspen zone below. The following were observed only in the spruce zone: *Sporobolus brevicalyx* Scribn., *Calamagrostis Langsdorffii* (Link) Trin., *C. Scribneri* Beal, *Agrostis humilis* Vas., *Poa reflexa* Vas. and Scribn., and *Festuca ovina pseudo-ovina;* while *Poa pratensis* L. was also collected in the aspen zone.

If we continue the comparison, and examine the species that occur in the aspen zone, we meet with a larger number of species of the same tribes that were observed at higher elevations, and with them there also occur some of the Chlorideae. Peculiar to this zone are: *Stipa minor* Scribn., *Muehlenbergia comata* Benth., *M. gracilis* Trin. and the var. *breviaristata* Vas., *Alopecurus aristulatus* Michx., *Sporobolus depauperatus* (Torr.) Scribn., *Agrostis exarata* Trin., *Trisetum montanum* Vas., *Koeleria cristata* Pers., *Glyceria americana* (Torr.), *G. Holmii* Beal, *Poa annua* L., *P. nemoralis* L., *Festuca Thurberi* Vas., *Bromus breviaristatus* Thurb., *B. Richardsonis* Link, *Hordeum nodosum* L., *Elymus Sitanion* Schult., and *E. brevifolius* (Sm.). Besides these there are a few species which occur here, but which more properly belong to the plains, where they are more abundant and more typically developed. These are *Agrostis scabra* Willd., *Schedonnardus texanus* Steud., *Bouteloua oligostachya* Torr., and *Atropis airoides* (Nutt.). The number of species of Gramineae observed in the mountainous regions, from the aspen zone to the summits, averages about 50, among which the Chlorideae are rather scantily represented.

Descending to the plains, at an elevation of 1500^{m} about 40 species belonging to the same tribes are found; the Andropogoneae and Paniceae are added; and the Chlorideae abound. The following species are very frequent: *Panicum virgatum* L., *P. capillare* L., *Aristida fasciculata* Torr., *Stipa comata* Trin. and Rupr., *S. viridula* Trin., *Eriocoma cuspidata* Nutt., *Cenchrus tribuloides* L., *Sporobolus cryptandrus* Muehl., *S. asperifolius* Thurb., *S. airoides* Torr., *Calamovilfa longifolia* (Hook.) Hack., *Agrostis scabra* Willd., *A. intermedia* Scribn., *A. alba* L., *Schedonnardus texanus* Steud., *Bouteloua oligostachya* Torr., *B. racemosa* Lag., *Buchloë dactyloides* Engelm., *Munroa squarrosa* (Nutt.) Torr., *Distichlis spicata* (L.) Grne., *Atropis airoides* (Nutt.), *Poa Buckleyana* Nash, *Festuca tenella* Willd., *Agro-*

pyrum occidentale Scribn. vars. *mollis* and *vivipara, A. tenerum* Vas., *A. spicatum* Pursh, *Hordeum jubatum* L., and *Elymus canadensis* L. Some others are more scattered, for instance: *Andropogon furcatus* Muehl., *Echinochloa crus-galli* (L.) Beauv., *Muehlenbergia glomerata* Trin., *Lycurus phleoides* H. B. K., *Setaria glauca* L., *Bouteloua prostrata* Lag., *Diplachne fascicularis* (Lam.) Beauv., *Eragrostis major* Host., etc.

This grass vegetation in the wooded belts and on the plains consists mostly of American types, and the very few species that are also represented in the Old World are mostly introduced, for instance: *Echinochloa crus-galli, Digitaria glabra, Setaria glauca, Eragrostis major*, and *Agrostis alba. Calamagrostis Langsdorffii*, which I found in the spruce zone on Mt. Massive, occurs also in the mountains of New England, Canada, Alaska, south to California, and is also an inhabitant of Europe and Asia. *Poa annua, P. nemoralis, P. pratensis*, and *Koeleria cristata*, widely distributed species in the Old World, especially in the lowlands of the cold temperate zone, are also represented in the aspen zone. *P. nemoralis* is very common and varies according to the substratum, whether dry rocks or rich soil, in thickets, along streams, etc.

In comparing the geographical distribution of these various species of Gramineae which occur in the alpine region, in the wooded belts of the mountains, and on the plains, it is noticeable that the genera of the alpine flora are more cosmopolitan than those of the lower levels. None of the genera of the alpine Gramineae are endemic, and about one-half of the species occur also in the Old World (cf. Table III). On the other hand, the presence of arctic and circumpolar species is characteristic of the alpine flora, species which may be regarded as remnants of an old glacial vegetation that migrated from the far north; but those endemic in Colorado may have developed in the alpine regions of these very mountains.

Let us now examine the grass vegetation of the alpine region of the Alps of Switzerland, the Pyrenees, the mountains of Norway, the Caucasus, and the Himalayas. In these mountains the tribes that occur in Colorado are found, besides the Phalarideae, of which *Hierochloa laxa* Br. has been reported from the Himalayas (5000^m), and *Anthoxanthum odoratum* L. from Switzerland and the Caucasus.

In the Alps of Switzerland the tribe Festuceae is the best represented, according to HEER.[3] There are four species of Festuca (*F. ovina* L., *F. pumila* All., *F. pilosa* Hall. fil., and *F. Halleri* Vill.) and five of Poa (*P. alpina* L., *P. caesia* Sm., *P. laxa* Hnke., *P. minor* Gaud., and *P. annua* L.). *Koeleria hirsuta* Gaud., *Sesleria coerulea* L., and *S. disticha* Pers. also are present. Four Aveneae occur here (*Avena distichophylla* Vill., *A. versicolor* Vill., *Deschampsia caespitosa* Beauv., and *Trisetum subspicatum* Beauv.); two small species of Agrostis (*A. rupestris* All. and *A. alpina* Scop.) represent, with *Phleum alpinum* L., the Agrostideae; while *Nardus stricta* L. is the only member of Hordeae, observed so far, in these regions. Of these species *Sesleria disticha* and *Poa laxa* have been recorded from the highest elevation (3000^{m}).

In the Pyrenees[4] the genera are about the same, with the addition of *Holcus caespitosus* Boiss. (Aveneae), *Molinia coerulea* Moench., and *Nardurus Lachenalii* Godr. (Festuceae). The Festuceae are here also best represented, numbering 17 species, among which the following are known also from Switzerland: *Sesleria disticha*, *Festuca Halleri*, *F. pumila*, *Poa laxa*, *P. caesia*, *P. minor*, and *P. alpina*. Among the Agrostideae, *Agrostis rupestris* and *A. alpina* are here accompanied by three other species: *A. setacea* Curt., *A. nevadensis* Boiss., and *A. capillaris* L., while *Phleum alpinum* is only known from the subalpine region of these mountains. The Aveneae are represented by *Deschampsia flexuosa*, while *D. caespitosa* occurs only at lower elevations; also by *Avena albinervis* Boiss., *A. Scheuchzerii* All., *Holcus caespitosus* Boiss., *Trisetum flavescens* Beauv., *T. velutinum* Boiss., *T. glaciale* Boiss., and *T. Gaudinianum* Boiss., while *T. subspicatum* does not reach the alpine region in these mountains. The Hordeae are also here only represented by *Nardus stricta*.

In the mountains of Norway[5] the alpine Gramineae number only 8 species: *Phleum alpinum*, *Aira alpina* L., *Trisetum subspicatum*, *Catabrosa algida* Fr., *Poa laxa*, *P. stricta* Lindeb., *P. flexuosa* Wahl., and *P. alpina*, all of which extend to the arctic region.

[3] HEER, O., Ueber die nivale Flora der Schweitz. 1883.

[4] D. MARIANO DEL AMO Y MORA, Flora Fanerogámica de la Peninsula Iberica. Granada 1:2. 1871.

[5] BLYTT, M. N., Norges Flora. Christiania. 1861.

According to MEYER[6] 22 Gramineae are alpine in the Caucasus. Of special interest are *Phleum alpinum, Avena versicolor, Deschampsia flexuosa, Trisetum flavescens, Poa alpina, Koeleria cristata,* and *Festuca ovina.* Besides these it is interesting to notice the occurrence of *Calamagrostis caucasica* Trin., *Briza media* L., *Poa altaica* Trin., *Colpodium Steveni* Trin., and *Hordeum pratense* Huds.

If we extend the comparison to the Himalayas,[7] we notice the presence of 5 alpine species which occur also in Colorado (cf. Table III); also the occurrence of genera that are not represented in the other mountains, namely Hierochloa, Stipa, Deyeuxia, Danthonia, and Elymus (*E. sibiricus* L.). The very considerable elevation of 5500^m is in these mountains reached by *Trisetum subspicatum, Poa hirtiglumis* Hook. f., and *Elymus sibiricus* L.; from between 4500 and 5100^m the following are recorded: *Hierchloa laxa* Br., *Agrostis inaequiglumis* Griseb., *Deyeuxia compacta* Munro, *D. nivicola* Hook. f., *D. pulchella* Hook. f., *Deschampsia caespitosa, Catabrosa sikkimensis* Stapf, *Poa alpina* L., *P. attenuata* Trin., *P. nemoralis* L., *P. flexuosa* Wahl., *P. tremula* Stapf, and *Festuca valesiaca* Schleich. Two species of Stipa (*S. concinna* Hook. and *S. mongolica* Turcz.) ascend to an elevation of 4000^m.

The Himalayas are thus much richer in alpine types than any of the other mountains, a fact that becomes still more manifest when we compare the representatives of the other families. Nevertheless, the alpine Gramineae of the Himalayas do not possess any type which from a biologic point of view deviates to any great extent from those of Colorado. For instance, Stipa and Elymus are really the only alpine genera in which the structure of spikelets is quite distinct from that of most of the others. It seems altogether as if the alpine Gramineae are remarkably uniform in habit, and in floral structure.

In speaking of Colorado especially, we have not in the alpine region a single type that may be compared with Buchloë, Munroa, Sporobolus, or Distichlis from the lowlands. The alpine representatives are perennial, except *Deschampsia calycina;* they are mostly

[6] MEYER, Verzeichniss der Pflanzen, welche im Caucasus etc., gefunden sind. St. Petersburg. 1831.

[7] HOOKER, J. D., Flora of British India. London. 1894. Vol. 6.

caespitose or sometimes stoloniferous, but with simple culms, and with an inflorescence (spicate or paniculate) of the usual composition. The empty glumes show no peculiar structure, and the flowering glume is either awned or awnless, and not in any way different from the usual structure among grasses in general. The average height of these alpine Gramineae is in some cases much less, in other cases about the same as that of lowland species of the same genera. *Poa Lettermanii*, the species of Agrostis, and *Festuca ovina* are mere dwarfs, but *Agropyrum Scribneri* reaches a height of 50^{cm}, even at an elevation of 4000^{m}. *Agropyrum violaceum* at the same altitude has culms about 40^{cm} high; and the culms of *Deschampsia caespitosa*, *Calamagrostis purpurascens*, and *Poa gracillima* reach about the same height. In habit the alpine Gramineae do not exhibit any characteristics which might indicate the extreme conditions under which they live. The same is the case with those grasses that occur in the arctic region, where we meet with several species that do not occur farther south, but the habit of these is of the same general kind. It is very different with the representatives of most of the dicotyledonous families from the alpine and arctic regions; in these the habit is frequently so peculiar and characteristic that they are readily recognized as being either alpine or arctic. In other words, the monocotyledons, at least the Glumiflorae, do not appear to be influenced to any great extent by climate and soil, as are most of the dicotyledons, at least not in regard to their general habit in alpine or arctic regions.

An examination of the internal structure of these alpine species from Colorado will demonstrate probable characteristics in structure; "probable," because I am not in a position to make any comparison with species from other alpine regions. It is my intention merely to present these anatomical data for future comparison, when someone may feel induced to investigate the grass vegetation of other mountains, and especially from high altitudes. I have examined roots, culms, and leaves. The leaf structure might have been sufficient, and, as already stated, most authors have so far confined their work to the leaves alone. However, it does not appear to me that the structure of culms and roots should be neglected altogether, and especially not when dealing with plants that are able to persist under such extreme conditions.

The roots

In considering the internal structure of roots that are simply nutritive and of no long duration (perhaps only one season), we must not expect to find great modifications. In regard to the Gramineae we have learned from KLINGE'S[8] interesting paper that certain modifications may be observed in the structure of the cortex, whether persisting or collapsing, whether homogeneous or differentiated as distinct zones of parenchymatic or stereomatic strata; also in the thickening of the endodermis, and in the structure of the pericambium, whether it is continuous or interrupted by the proto-hadrome. The presence or absence of an exodermis also seems to be worth mention, and the structure of the parenchyma in the stele, which sometimes represents a central pith. Much attention has been given to the position of the proto-hadrome vessels, whether they are inside the pericambium or border directly on the endodermis. In some instances all these vessels have been observed to occupy the same position in reference to the pericambium; but in other instances a variation has been noticed, where only some of the proto-hadrome vessels had broken through the pericambium. In studying root structures of different plants, especially of monocotyledons, one gets the impression that the continuity or interruption of the pericambium is of some importance and constitutes a good anatomical character. In very many roots I have found a constantly continuous pericambium or a constantly interrupted one; but on the other hand, as shown in Eriocaulon and Carex,[9] there are also cases where this structure is not constant, but varies from the base to the apex of the same root. This peculiarity I noticed by making consecutive sections of a number of roots, and it appears therefore as if the structure of the pericambium, so far as concerns its continuity or interruption, is not a character to be depended upon. In *Deschampsia caespitosa* and *Festuca ovina* from Europe, KLINGE (*l. c.*, p. 56) observed the proto-hadrome vessels bordering on the endodermis; while in these same species from Colorado all the vessels were found to be inside the pericam-

[8] KLINGE, Vergleichend histiologische Untersuchung der Gramineen- und Cyperaceen-Wurzeln insbesondere der Wurzel-Leitbündel. Mém. Acad. Imp. St. Petersbourg VII. **26**: No. 12. 1879.

[9] BOT. GAZETTE **31**: 17. 1901; and Am. Journn. Sci. **10**: 278. 1900.

bium. Such discrepancies often occur, but they are hardly of any importance.

In the alpine Gramineae from Colorado the root structure is very uniform. The epidermis is hairy in all the species; a thin-walled exodermis was observed only in *Agropyrum violaceum*. The cortical parenchyma is mostly thin-walled and solid, but a radial collapsing was noticed in the species of Poa, with the exception of *P. alpina*, in Trisetum, and in Deschampsia. In the species of Agropyrum the peripheral strata of the cortex are stereomatic, and persistent in comparison with the inner, which are thin-walled and collapsed. The endodermis is generally thick-walled (*figs. 1–5, End*), representing a typical U-endodermis, or an O-endodermis, as was observed in specimens of *Poa alpina* from bowlder fields. The pericambium was found to be continuous in all the species, and it is generally thin-walled; but in the species of Agrostis (*fig. 2*), Calamagrostis, Trisetum, and in *Poa gracillima* it is more or less thick-walled. It consists mostly of a single layer, but in the species of Agropyrum (*fig. 5*) and Avena two or three layers are developed outside the proto-hadrome vessels. The number of hadromatic rays is of course very variable; in the thick roots of Trisetum, Deschampsia, Calamagrostis, Avena, and Agropyrum there may be as many as fifteen rays, but with mostly a single proto-hadrome vessel in each ray. In the species of Agrostis and Festuca the hadrome extends to the center of the stele, while in the others a central pith is developed. This pith is quite broad, and often conspicuously thick-walled, as in Trisetum, Agropyrum, Avena, and Calamagrostis.

It is interesting to note that in some cases the root structure corresponds with the nature of the substratum. For instance, in *Poa Lettermanni*, which I found growing in wet moss near the snowbanks, the root structure resembles that of a hydrophilous plant, with open cortex, thick-walled endodermis, and thin-walled pericambium. In the species of Agropyrum from very dry, stony soil, the peripheral strata of the cortex are stereomatic. In *Calamagrostis purpurascens* from similar stations there is a very compact cortex, a heavily thickened endodermis, a thick-walled pericambium, and a broad central, very thick-walled pith. A similar, very solid structure is also characteristic of the species of Festuca and

Agrostis, inhabitants of dry soil among bowlders. The roots of these species thus show in general the structure of xerophytes. But in *Poa alpina* no such distinction seems feasible, since the structure is identical whether the specimens are from wet soil in thickets of willows along mountain brooks, or from dry soil among bowlders.

The culm

In describing the structure of the culm, attention must be given to the distribution of the mechanical tissue (stereome), to the minor structure and disposition of the mestome strands, and finally to the structure of the cortical parenchyma. In the character of the stereome our alpine Gramineae represent the type in which a circular band of this tissue (in cross-sections) is in contact with all the mestome bundles; it is the eleventh type of SCHWENDENER[10] and is the one most frequently observed in the Gramineae. While the principal feature of this type is that all the mestome strands are in contact with the mechanical tissue, some modifications are to be observed in regard to the relative development or strength of the stereome, especially in cases where the mestome bundles occur in different sizes, and in more than one circular band. Five very distinct modifications were observed in our alpine species, which may be readily distinguished by the accompanying figures, which I have drawn in a schematic way. The black represents the stereome; the peripheral white zone the cortex; the central white zone the pith; the orbicular and oval rings the mestome strands.

In these figures, *A* represents the most simple structure, where there are only five mestome strands, all the same size and outline (oval), and all imbedded in the stereome, which extends to epidermis, thus forming a strong, hypodermal support outside the leptome (*Agrostis canina*, var.). In *B* there are four large, oval mestome strands, alternating with four much smaller ones, which are orbicular in transverse section, and they are all surrounded by stereome, which only extends to the epidermis outside the larger ones (*Poa Lettermanni*, *P. alpina* from Long's Peak, and *Agrostis varians*). In *C* (*Poa rupicola*) there is also one band of mestome bundles, composed of

[10] SCHWENDENER, Das mechanische Princip im anatomischen Bau der Monocotylen 60. Leipzig. 1874.

larger (oval) and smaller (orbicular) ones; and hypodermal stereome occurs outside each of the mestome strands, but is only in contact with the leptome side of the larger ones; the smaller strands only touch the inner stereome with their hadrome side. When two concentric bands of mestome bundles occur, the peripheral ones are the smallest and are orbicular in cross-section; the inner ones are either

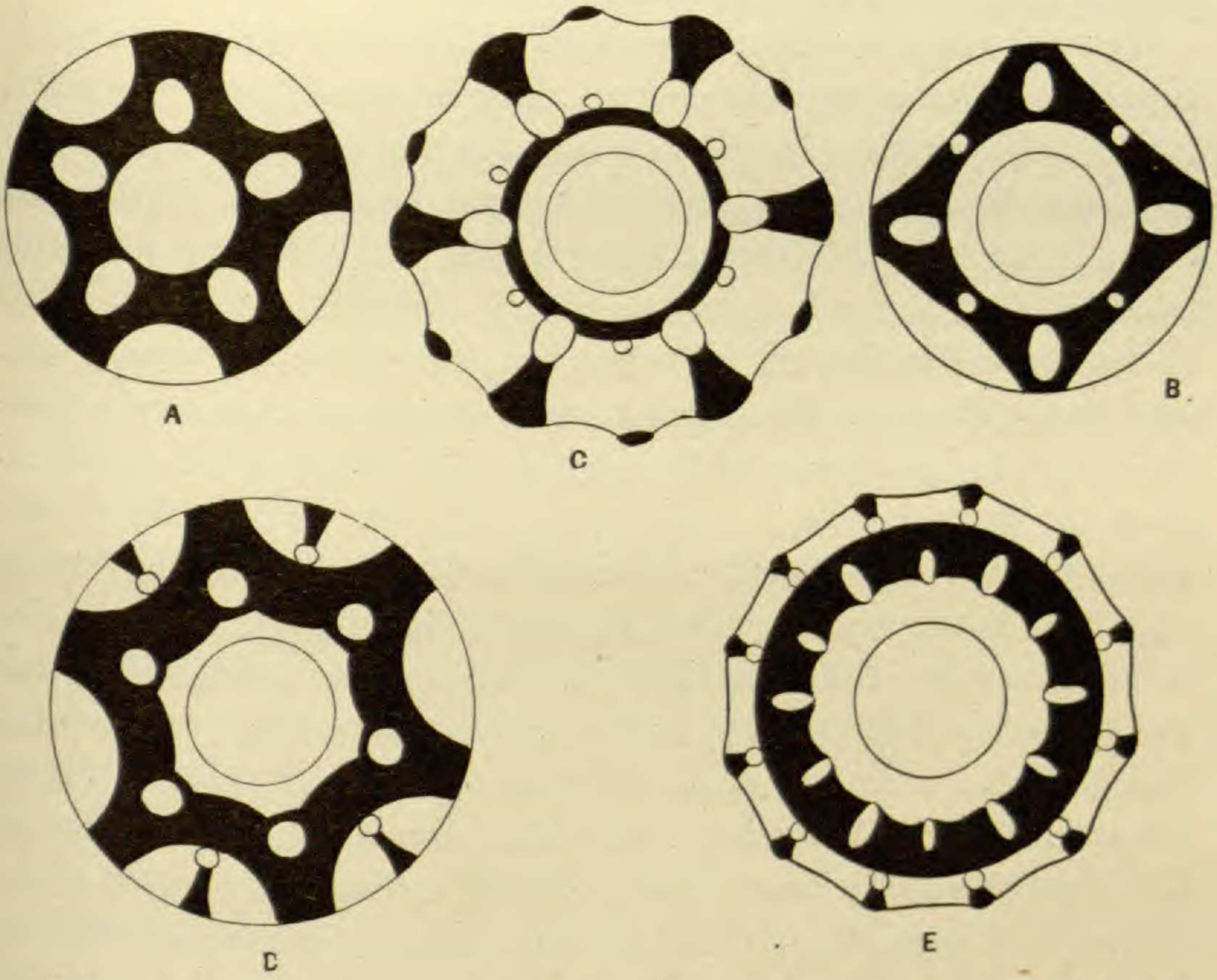

Diagram showing the structure of the culms of *Agrostis canina* var. (*A*), *Poa Lettermanni* (*B*), *P. rupicola* (*C*), *P. alpina* (*D*), and *Agropyrum violaceum* (*E*).

orbicular (*D*) or oval, often representing two sizes, as shown in *E*. In these culms (*D* and *E*) the stereome shows two well-marked modifications. It constitutes a mechanical support on the leptome side of all the mestome strands in *D;* while in *E* this hypodermal support is confined to the peripheral strands alone—those of the inner band (*E*) are imbedded in a zone of stereome, which does not extend to epidermis. The structure illustrated by *E* was observed in *Calamagrostis purpurascens*, *Agropyrum violaceum*, and *Deschampsia caespitosa* from Graymont; while *D* is the most frequent structure exhibited by the remaining species, including *Poa alpina* from Mt. Kelso and *Deschampsia caespitosa from* Gray's Peak. These culms thus represent five types as to the occurrence of one or two bands of mestome bundles, and as to the distribution of the stereome as a circular band extending to the epidermis as hypodermal groups in contact with or separated from some of the mestome bundles (the latter case is illustrated in *C*).

The fact that two of these types (*D* and *E*) have been observed in one species (*Deschampsia caespitosa*), though from different elevations, seems to indicate that the structure may not be constant. The type *D* appears to be the most frequent in the alpine species of Colorado, and the most important difference between this and the three preceding (*A*, *B*, and *C*) depends upon the presence of two concentric bands of mestome bundles, all of which are supported by hypodermal stereome. The type *E* is more complicated on account of the inner mestome strands being of different size and lacking the hypodermal stereome, and this type, as stated above, was observed in *Agropyrum violaceum*. If this structure be compared with that of the French species of Agropyrum described by DUVAL-JOUVE, it is observed that it does not agree with any of them. The species examined by this author were lowland species, and several were maritime. Characteristic of these species is the occurrence of hypodermal stereome outside the smaller as well as the larger mestome strands; also in some species the inner band may be located nearer the center of the culm, a considerable distance from the stereomatic zone. In other words, the lowland species of Agropyrum in France represent actually an entirely distinct type of structure, which corresponds with the twelfth type of SCHWENDENER (*l. c.*), in which the inner mestome strands are in the pith, some distance from the stereomatic cylinder.

The minor structure of the mestome strands in our alpine species agrees in most respects with that of other Gramineae. It has been shown that some variation occurs in the outline of cross-sections, some being orbicular (especially the smaller ones), and the larger ones usually oval. The leptome and hadrome differ in no way from that of other species from lower elevations. A more or less thick-

[11] DUVAL-JOUVE, Etude anatomique de quelques Graminées et en particulier des Agropyrum de l'Hérault. Mém. Acad. Sci. Montpellier. Paris. 1870.

walled mestome sheath was observed in all the alpine Gramineae, and these species may thus be added to the list given by SCHWENDENER[12] in his paper on mestome sheaths. However, the presence or absence of the mestome sheath, as already pointed out by SCHWENDENER (*l. c.*, p. 415), is merely of taxonomic importance. This may be readily seen from his list, according to which this sheath is not developed in any of the species of Andropogoneae and Maydeae, or in certain genera of the Paniceae (Paspalum, Pennisetum, and Setaria). The fact that it occurs in some species of Panicum (*P. miliaceum*, *P. capillare*, *P. proliferum*), but not in others (*P. sanguinale*, *P. plicatum*, *P. colonum*, etc.), seems to indicate that these species represent very distinct types within the genus, as shown also by the external structure of their spikelets. The same conclusion may be drawn from the fact that the species of Aristida in which I observed a double parenchyma sheath,[13] but no mestome sheath, differ in a marked degree from those which possess this sheath, and in which only a single parenchyma sheath is developed; we have here to deal with a taxonomic, and not with an epharmonic character. By studying the anatomy of a number of Gramineae allied to or associated with Aristida, I found a mestome sheath constantly developed, whether the material was collected on the plains, the prairies, in woodlands, or in marshes. If on the other hand the structure of the mestome sheath is examined, some kind of modification in the thickening of the cell walls is noticed, which evidently constitutes an epharmonic character; in the alpine species this sheath was generally observed to be quite thick-walled. The presence or absence of thick-walled mestome parenchyma as a stratum between the leptome and the hadrome is to be considered only of taxonomic importance; such parenchyma was not observed in *Poa Lettermanni*, *P. gracillima*, *P. rupicola*, or in the species of Festuca and Avena, but in all the others.

Of much greater interest, however, is the structure of the cortical parenchyma. This tissue is very compact in these Gramineae with the exception only of *Poa Fendleriana*, *P. gracillima*, and *Phleum alpinum*. It is either developed as a palisade tissue of several layers

[12] SCHWENDENER, Die Mestomscheiden der Gramineenblätter. Sitgungsber. Berliner Akad. Wiss. 413. 1890.

[13] HOLM, THEO. Some new anatomical characters for certain Gramineae. Beih. Bot. Centralbl. 11:—. 1901.

(*fig. 6, C*) or as a homogeneous tissue of roundish cells (in cross-section). The former structure is the most frequent, and especially well represented in *Poa rupicola*, *P. Lettermanni* (*fig. 6*), and *Agrostis canina;* the latter structure was observed in *Agrostis varians*, *Poa flexuosa*, Agropyrum, Calamagrostis, Deschampsia, and Festuca.

We will finally consider the structure of the cuticle and epidermis. The cuticle was observed to be smooth and quite thick in all the species, even in the densely hairy Trisetum. The epidermis is scabrous in Calamagrostis, hairy in Trisetum, but glabrous in the others. Some slight variation in the structure of the cell walls was noticed; the outer wall, for instance, is quite thick as compared with the inner and the radial, and this structure seems to be the most frequent. But in *Agrostis canina*, *Poa rupicola*, *Phleum alpinum*, and *Agropyrum violaceum* all the cell walls of epidermis were equally and quite heavily thickened.

A very firm structure is thus exhibited by the culms of our alpine Gramineae, so far as concerns the mechanical tissue and the dense cortical parenchyma covered by a thick-walled epidermis. It is also interesting to notice that the cortex generally contains much chlorophyll, and that the cells are developed as typical palisades, thus being able to perform the function of the chlorenchyma in the leaves. The modifications in structure in the culms depend mostly upon the distribution of the stereome, and upon the mestome strands (their relative size, their mechanical support, and their disposition in one or two concentric bands). The pith, on the other hand, shows no deviation from the most common structure known in this family; it was constantly found to be thin-walled and broken in the center, and with no deposits of starch.

The leaves

In the leaves the epidermis and chlorenchyma offer some distinctions of importance, and much more so than the stereome, at least in the alpine species. However, the structure is very uniform, and does not exhibit any such prominent epharmonic characters as are so well known from species of the lowlands, the plains, and the prairies. In the alpine species the leaf structure is very firm throughout; there are no wide intercellular spaces in the chlorenchyma, and no water-storage tissue surrounding the veins. The distribution of the stereome is mainly the same in all the species and rather scantily represented as compared with the culm. The mestome strands are constantly arranged in a single plane and are very uniform in structure.

In the epidermis the outer cell wall is generally quite thick on the dorsal face, but less so on the ventral; the cuticle is smooth, and very distinct in all the species. The characteristic bulliform cells between the mestome strands on the upper face of the blade were observed in all the species, but they are not very large, and are sometimes confined to a single group, one on each side of the midrib, as in *Poa Lettermanni*, *P. flexuosa*, *P. gracillima*, and *P. rupicola*; in the other species there may be four to six or even a larger number of groups in the lateral parts of the leaf blade. In *Poa Lettermanni* (*figs. 7, 8*) the leaves are glabrous on both faces, but in the other species they are generally a little scabrous from small, obtuse papillae. Pointed, prickle-like projections occur in Festuca, Agrostis, *Poa rupicola*, *P. Fendleriana*, and *P. alpina* from Long's Peak. Hairs are not frequent, but were observed on the ventral face of the blade in *Poa gracillima*, Calamagrostis, and Avena, and on both faces in Trisetum and *Agropyrum Scribneri*. With the exception of *Trisetum subspicatum*, which may be called densely hairy, the hairs in the other Gramineae are so scattered that they are often hardly visible to the naked eye.

The stomata (*fig. 7*) occur mostly on both faces of the blade, but as a rule are most frequent on the ventral face; in some species of Poa, *Agropyrum Scribneri*, Calamagrostis, and Trisetum they are confined to the ventral face. They are usually sunk, and sometimes covered by papillae or hairs, and they occur especially on the sides of the furrows between the mestome bundles. Their position in reference to the surface may sometimes vary on the same leaf; for instance, in *Agropyrum violaceum* they are free on the ventral face, but sunk on the dorsal, while the opposite is true of Avena; in *Deschampsia caespitosa* they are level with the epidermis, and not covered by the papillae. Otherwise the structure of the epidermis offers no points of particular interest.

The stereome is poorly represented in most of these species, and occurs often only as a very small hypodermal strand outside the larger mestome bundles (*fig. 8*) and not in contact with them; it is better developed in the margins of the leaves. The mestome strands show the same structure in regard to the leptome and hadrome as observed in the culm; there is also the same variation from oval to orbicular (in cross-section), and the mestome sheath is typically developed with the inner cell wall heavily thickened. Outside the mestome sheath the ordinary thin-walled parenchyma sheath is found mostly containing some chlorophyll. I have not observed a single instance in these alpine species where mestome strands occurred beneath the bulliform cells; but in *Deschampsia caespitosa* from Graymont, at a much lower elevation, some few very fine veins were observed between the larger ones, thus being located directly underneath the bulliform cells. It might be mentioned at the same time that DUVAL-JOUVE (*l. c., pl. 16, fig. 5*) figures a leaf of a French specimen in which a very small mestome strand occurs between each of the two larger veins, just beneath the bulliform cells.

The chlorenchyma is very compact in these alpine species, and is mostly developed as a palisade tissue. In *Poa Lettermanni*, however, it is developed as palisades only around the mestome strands, radiating toward their center, while in the other portions of the leaf this tissue consists of much shorter and roundish cells (*figs. 7, 8*). In *Poa flexuosa* there are no palisades at all; in Phleum the cells are hardly high enough to be called palisades, even if some distinction may be noticed between the ventral and dorsal portion of the chlorenchyma. In all the other species the chlorenchyma constitutes a homogeneous palisade tissue, vertical to the surface or radiating toward the center of the mestome bundles. It is a very compact tissue throughout the leaf blade, and rich in chlorophyll.

The leaves of the alpine Gramineae are mostly erect, though not exactly vertical, and are frequently conduplicate or with the margins involute; they are seldom spreading or perfectly flat. In this way they agree to some extent with the species from the plains, although the internal structure is very different, at least in certain genera. In the alpine species the leaves are often furrowed on the ventral face, but not to the extent so commonly observed in the lowland species, in those that inhabit the plains for instance. This may perhaps be the reason why the stomata in the alpine species are so much deeper than in those from the lowlands, where they are level with the epidermis, but protected by the more ample covering of papillae or hairs, and also by the greater depth of the furrows. In the leaves of the lowland species the stereome is better represented, the bulliform cells generally larger, and frequently accompanied by several strata of a colorless tissue, the so-called water-storage tissue, which is not developed in the alpine species. But in the chlorenchyma of the Gramineae from the plains and prairies we find a more or less homogeneous tissue of palisades occupying the position described above. Finally the fact must be mentioned that the stomata being most frequent on the ventral face of the leaf is a feature the alpine Gramineae have in common with nearly all those which I have examined from the lowlands, and especially those from the plains and prairies, with the exception of Sporobolus, Munroa, and Calamovilfa. In the woodland types of Muehlenbergia the stomata are almost equally distributed on both faces of the leaf blade; while in the species of the same genus from dry, rocky mountain slopes, the stomata are confined to the ventral face and protected by the folding of the blade. In species from wet soil, meadows, or swamps, the stomata are most frequent on the dorsal face in Leersia; while in Amphicarpum from moist pine barrens they are distributed over both faces, though most numerous on the ventral; in *Uniola latifolia* from shaded slopes the stomata occur only on the ventral face, and this same disposition is to be found also in *Pleuropogon Sabinei* from arctic swamps. DUVAL-JOUVE, who has examined a large number of Gramineae,[14] speaks of the difficulty of giving any precise information about the distribution of stomata in this family. He observed also that the ventral face of the blade is sometimes the only one where the stomata occur, but at the same time he noticed that a torsion of the leaf took place, thus exposing the dorsal face to the sun instead of the ventral. In this way the stomata become well protected, but in our alpine types the only protection seems to depend upon the folding of the blade, conduplicate or with the margins involute.

The leaf structure of alpine plants has been described and explained by several authors, but the Gramineae have been neglected, and evidently because the narrow leaves appear to be more uniform in

[14] DUVAL-JOUVE, Histotaxie des feuilles de Graminées. Ann. Sci. Nat. Bot. VI. 1:314.

structure and apparently of less interest. I am not in the position to draw any anatomical comparison, therefore, between the species from the Rocky Mountains and those from other alpine regions. The alpine types which have been treated and studied in Europe are nearly all dicotyledons, and the results are not quite comparable to those derived from the study of our Gramineae. According to BONNIER[15] and WAGNER,[16] the palisade tissue should be far better developed in the alpine forms (dicotyledons) than in those from the lowlands; the leaves should be thicker, and the structure more open on account of the wider intercellular spaces; also the alpine leaves should be more thoroughly dorsiventral, with stomata sometimes more abundant on the ventral than on the dorsal face; the guard cells should be level with the epidermis except in species with evergreen leaves (Ericaceae, etc.).

These distinctions are not to be observed in the Gramineae. We have seen that in the alpine representatives of this family the leaves are not dorsiventral; the palisade tissue is not developed to any greater extent than in the lowland species; the chlorenchyma is not open, on the contrary it is very compact; also the stomata are not level with the epidermis but mostly sunken. It seems almost safe to conclude that the epharmonic characters are much less pronounced in the alpine Gramineae than in the dicotyledons from similar high situations, when compared with the corresponding lowland types. Much would be learned, however, by examining alpine Gramineae from other parts of the world, and especially other genera and species than those described in the preceding pages. Also the study of alpine types ought not to be restricted to a mere consideration of the foliar organs, even if these unquestionably are the most important; the structure of stem and root ought not to be excluded altogether, as is frequently or nearly always the case.

Conclusions

We have seen that the alpine Gramineae of Colorado constitute an assemblage of very distinct geographical types; some that are only

[15] BONNIER, GASTON, Cultures expérimentales dans les hautes altitudes. Compt. Rend. Acad. Sci. 1890; Etude expérimentale sur l'influence du climat alpin sur la végétation et les fonctions des plantes. Bull. Soc. Bot. France **1888**:436.

[16] WAGNER, Zur Kenntniss des Blattbaues der Alpenpflanzen und dessen biologischer Bedeutung. Sitgungsber. K. Akad. Wiss. Wien **101**:59. 1892.

known from the alpine regions of this country; others that are known also from the higher mountains of Eurasia; some that have reached the polar regions, among which several are circumpolar; and finally some that occur also at lower altitudes in these same mountains. The alpine genera seem to be more cosmopolitan than those observed at lower levels; as a matter of fact none of these genera of Gramineae are endemic to this country, and none of the alpine genera of Europe and Asia are endemic to those countries.

The habit and floral structures of the alpine Gramineae of Colorado are remarkably uniform and simple, when compared with some of the other species and genera from the lowlands. Corresponding with this uniformity in habit, we meet with no extraordinary development of any of the tissues. The anatomical structure is rather simple, and neither the stereome, nor the chlorenchyma, nor the stomata exhibit any feature that might be looked upon as characteristic of an alpine type. In this respect the alpine Gramineae differ from most of the other families, not so much, however, from the Cyperaceae as from the Juncaceae (Luzula and Juncus), and especially from the dicotyledons. The habit and internal structure of the alpine dicotyledons of Colorado are very distinct from those of their representatives which thrive at lower elevations in mountains or on the plains and prairies; very prominent distinctions of this kind I have observed in a number of alpine genera, as Ranunculus, Trifolium, Claytonia, Stellaria, Synthyris, Mertensia, Primula, etc. Whatever conclusions may be drawn from the various treatments of alpine plants in general, and especially in regard to "adaptations," it must be borne in mind that the monocotyledons have so far been almost entirely ignored, although they are certainly of no small interest on account of their frequent occurrence and very wide distribution in the high alpine regions. It seems thus very unsafe to describe the alpine leaf "in general" without including the Gramineae, and for this purpose the present paper may be of some interest to future students of "alpine structures."

BROOKLAND, D. C.

EXPLANATION OF PLATE XXX

FIG. 1.—Cross-section of root stele of *Poa Lettermanni*: *End*, endodermis; *P*, pericambium; *PL*, proto-leptome; *PH*, proto-hadrome. ×560.

FIG. 2.—Root stele of *Agrostis canina* var.; letters as above. ×560.

FIG. 3.—Root stele of *Festuca ovina;* letters as above. ×560.

FIG. 4.—Root stele of *Poa flexuosa;* letters as above. ×560.

FIG. 5.—Part of root stele of *Agropyrum Scribneri;* letters as above. ×560.

FIG. 6.—Cross-section of part of culm of *Poa Lettermanni*, showing epidermis (*Ep*), cortex (*C*), stereome (*St*), and two mestome strands with their mestome sheaths (*MS*). ×400.

FIG. 7.—Same species; cross-section of leaf, showing ventral epidermis (*Ep*) with a stoma, and two strata of chlorenchyma (*C*). ×400.

FIG. 8.—Same species; cross-section of leaf, showing dorsal epidermis (*Ep*), hypodermal stereome (*St*), and chlorenchyma (*Ca*). ×400.